CHOICE BETWEEN CONSTANT AND VARIABLE ALTERNATIVES BY RATS: EFFECTS OF DIFFERENT REINFORCER AMOUNTS AND ENERGY BUDGETS

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Two experiments, using rats as subjects, investigated the effect of different reinforcer amounts and energy budgets on choice between constant and variable alternatives under a closed economy. Rats were housed in the chamber and were exposed to a modified concurrent-chains schedule in which the choice phase was separated from a rest phase during which the rats could engage in other activities. In the choice phase, a single variable-interval schedule arranged entry into one of two equal terminal links (fixed-interval schedules). The constant terminal link ended with the delivery of a fixed number of food pellets (two or three, depending on the condition), whereas the variable terminal link ended with a variable number of food pellets (means of two or three, depending on the condition). Energy budget was defined as positive when body weights were over 90% of free-feeding weights, and as negative when they were under 80% of free-feeding weights. The different body weights were produced by varying the duration of the equal terminal-link schedules within daily 3-hr sessions. In Experiment 1, rats chose between a constant and a variable three pellets under both energy budgets. Rats preferred the constant three pellets more under the positive energy budget, whereas they were indifferent under the negative energy budget. In Experiment 2, rats chose between a constant three pellets and a variable two pellets, and chose between a constant two pellets and a variable three pellets under both energy budgets. The rats strongly preferred the constant three pellets over the variable two pellets under both energy budgets. In contrast, rats preferred the variable three pellets over the constant two pellets only under the negative energy budget, whereas they were indifferent under the positive energy budget. These results indicate that rats' choices are sensitive to the difference in reinforcer amounts and to the energy budgets defined by the level of body weight. The present results are consistent with those obtained with small granivorous birds as well as with the predictions of a recent risk-sensitive foraging theory.

Key words: choice, risk, energy budgets, body weights, reinforcer amounts, lever press, rats

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When foragers are faced with variable food resources, how do they deal with the variability? To address this question, psychologists and biologists have studied animals' choice under conditions in which variability in delay to food and variability in amount of food were manipulated in laboratory and field settings (see Kacelnik & Bateson, 1996, for a review). When variability is in the delay to food, foragers prefer a variable delay over a constant delay to equal amounts of food (e.g., Bateson & Kacelnik, 1995; Cicerone, 1976; Logan, 1965; Zabludoff, Wecker, & Caraco, 1988). However, when the variability is in the amount of food, results with different species, in which expected energy budgets or energy intake was manipulated, have been inconsistent. When the expected energy budget was positive, foragers consistently preferred the constant amount of food; that is, they were risk averse (e.g., Barkan, 1990, black-capped chickadees; Barnard & Brown, 1985, common shrews; Caraco, Martindale, & Whittam, 1980, yellow-eyed juncos; Hastjarjo, Silberberg, & Hursh, 1990, rats). In contrast, when the expected energy budget was negative, small granivorous birds and common shrews preferred the variable amount of food; that is, they were risk prone (e.g., Barnard & Brown, 1985; Caraco et al., 1980). However, pigeons, elephant shrews, and rats were indifferent between the variable and constant food amounts (e.g., Hamm & Shettleworth, 1987, pigeons; Hastjarjo et al., 1990, rats; Kagel, MacDonald, Battalio, White, & Green, 1986, rats; Lawes & Perrin, 1995, elephant shrews), and rats preferred the constant amount of food; that is, they were risk averse (e.g., Battalio, Kagel, & MacDonald, 1985).

For example, Caraco et al. (1980) present-
ed yellow-eyed juncos with a choice between
two feeding stations that differed in the vari-
ability of reinforcers (i.e., millet seeds), but
with the same mean, in a discrete-trials pro-
cedure. They found that the juncos tended to
choose the variable reinforcer when their ex-
pected energy intake fell short of daily energy
requirements (i.e., negative energy budget),
whereas the birds tended to choose the con-
stant reinforcer when expected energy intake
exceeded daily energy requirements (i.e.,
positive energy budget). The juncos' tenden-
cy to choose the variable amount of food (i.e.,
risk-sensitive foraging preferences) thus de-
pended on expected energy budgets (i.e., the
energy budget rule). In this procedure, ex-
pected energy budgets were manipulated by
varying deprivation periods (1 hr or 4 hr) at
the start of a session and the intertrial inter-
val (30 s or 60 s) during the session. As such,
each experimental session consisted of a dep-
rivation period and 40 trials of training and
testing, and the juncos were fed ad lib after
each session.

In contrast, Hamm and Shettleworth
(1987, Experiment 1), using a concurrent
(i.e., choice) schedule with time allocation,
arranged a procedure in which the variable-
interval (VI) values of the concurrent sched-
ules were increased. Hamm and Shettleworth
assumed that increasing the VI values (from
VI 20 s to VI 180 s) corresponded to moving
the expected energy budget toward negative.
The pigeons obtained nearly all the food they
needed to maintain their body weights at
85% of their free-feeding weights during ex-
perimental sessions. The pigeons were pre-
sented with a choice between constant and
variable outcomes. In all conditions, the pi-
geons chose the constant and variable out-
comes about equally often (i.e., they were in-
different).

As represented in these studies, there are
several procedural differences across studies
using different species, such as different pro-
cedures for manipulating expected energy
budgets (e.g., deprivation periods, number of
trials, or intertrial intervals), different choice
procedures (discrete-trials and free-operant
procedures), and different economic condi-
tions (open and closed economies). These
factors were mixed in the above-mentioned
studies, and the effects of these factors on

choice of variability in amount of food have
not been studied separately (see Kacelnik &
Bateson, 1996, for a review).

Although there have been several different
procedures for manipulating expected ener-
gy budgets, the notion of expected energy
budgets does not correspond to any one spe-
cific procedure, and this may be a reason for
the inconsistent results obtained. Consider-
ing these procedural differences, the goal of
the present work was not to evaluate the ef-
fect per se of the procedures by which ex-
pected energy budgets were manipulated.
Rather, we attempted to determine the effect
of a procedure on choice when it resulted in
an increase or a decrease in the animal's
body weight. Changes in body weight may re-
veal a forager's energy reserves directly, and
these energy reserves seem to influence
choice of variability in amount of food (e.g.,
Snyderman, 1983). A few studies have re-
ferred to the resultant levels of body weight,
but they did not manipulate the level of body
weight so as to maintain it at particular per-
centages of free-feeding weight as a control-
ling factor for animals' choices of variability
in amount of food (e.g., Battalio et al., 1985;
Hastjarjo et al., 1990).

To study risk-sensitive foraging, it is neces-
sary, as Shettleworth (1988, 1989) pointed
out, to arrange a variety of operant laboratory
procedures to simulate various features of
natural environments. To incorporate some
of the features, the present study arranged a
procedure based on the standard concurrent-
chains schedule, which separated the forag-
ing (choice) phase and the rest phase during
which foragers engage in other activities
(Davison, 1992; Fantino, Abarca, & Ito, 1987;
Hanson & Green, 1989; Ito & Fantino, 1986;
cf. Lea, 1979). The present study focused on
changes in the level of body weight as a proxy
for differences in energy budget. The energy
budget rule (e.g., Caraco et al., 1980) pre-
dicts that under a positive energy budget (i.e.,
when foragers get enough food to meet their
daily energy requirements), rats would prefer
the constant amount of food, whereas under
a negative energy budget (i.e., when food is
scarce, thereby increasing the risk of starva-
tion), rats would prefer the variable amount
of food. Although the energy budget rule is
primarily concerned with the effect of star-
vation on choice, positive and negative ener-

gy budgets were defined for the present study by the level of body weight (over 90% or below 80% of free-feeding weights), which was manipulated by varying the length of equal terminal links of the modified concurrent-chains schedule in daily 3-hr sessions. The experiments examined whether rats' choices of the variable amount of food depended on the level of their body weights (or energy budget).

The variability in amount of food was based on a negative binomial distribution because this distribution is thought to represent the food distribution for many species in the wild (Iwasa, Higashi, & Yamamura, 1981; Pielou, 1969). In this type of distribution of food, there are many cases of no food and a few cases of highly concentrated food (Feller, 1968). The present study used a closed economy in which, in comparison to an open economy, no supplemental food was provided outside the experimental session (Hursh, 1980). Although most studies of risk-sensitive foraging have used an open economy, foraging animals in the wild are thought to live in habitats (or niches) that approximate closed economies (Collier, 1983; Hursh, 1980).

Experiment 1 studied choice between constant and variable amounts of food pellets with the same mean, whereas Experiment 2 studied choice between constant and variable amounts of food pellets that differed in mean number.

EXPERIMENT 1

METHOD

Subjects

Three male albino rats of the Wistar strain, approximately 3 months old at the beginning of the experiment, were housed individually in the experimental chamber under a 12:12 hr light/dark schedule. Rats were weighed before each session and maintained at under 80% or over 90% of their free-feeding body weights, depending on energy budget conditions. They had no experimental histories. Water was continuously available in the chamber.

Apparatus

Three identical chambers (31 cm by 31 cm by 31 cm) with three retractable levers each were used. The levers (2 cm by 0.2 cm) intruded 2 cm into the chamber and were mounted 5 cm above the floor on the front wall. The three levers were located 7 cm apart (center to center), and the center lever was located midway between the two side levers. Three 24-VDC lamps were located separately, 4.5 cm above each lever, on the front wall. The three levers could be retracted by a 24-VDC solenoid during which the lamp for the retracted lever was off. A minimum force of about 0.15 N was required to operate each lever. A food cup was located 1 cm above the floor on the center of the front wall and was illuminated by a 24-VDC lamp located 3 cm above the food cup for a prescribed period each time a reinforcer (a 45-mg food pellet) was delivered into the food cup. No houselight was used. A water bottle was mounted on the side wall. The whole chamber was enclosed in a sound-attenuating chest, and masking noise was provided by an exhaust fan. A 5-W fluorescent lamp mounted on the wall of the sound-attenuating chest was turned on during the light phase of the schedule. A microcomputer system (NEC PC-9801CV) controlled the experiment and recorded events.

Procedure

Preliminary training. Rats were initially trained to press the right lever by the method of successive approximations, and then presses on either the right or left lever were reinforced for several sessions. Only one lever (either right or left) was available at any time during preliminary training. Each daily session consisted of two components. One lever was assigned to each component according to a prescribed order. In each component, the lever available was presented a fixed number of times. This number differed between the right and left levers to provide the same number of reinforcers for each lever during preliminary training. Each lever press retracted the lever and produced a food pellet. Each daily session lasted until 100 reinforcers had been obtained.

Concurrent-chains schedule. Each rat was then housed in the chamber under a 12:12 hr light/dark cycle, and a concurrent-chains schedule was introduced. The present procedure modified the standard concurrent-chains schedule by adding a rest phase in
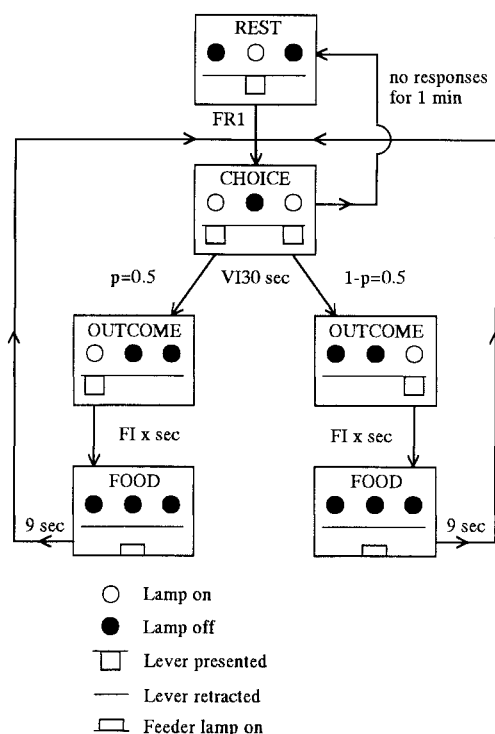
Fig. 1. A schematic representation of the modified concurrent-chains schedule used in the present experiments.

which the concurrent-chains schedule was not in effect (see Figure 1). This procedure was arranged to simulate foraging behavior in the wild by separating the foraging (choice) phase and the rest phase during which rats may engage in other activities. The experiment was conducted during the dark phase from 5:00 p.m. to 8:00 p.m. (3 hr).

At the beginning of each session, only the center lever was available (the rest phase). If a rat pressed the center lever, the center lever was retracted, the lamp for the center lever was turned off, and the two side levers were inserted (the choice phase) and their lamps turned on. Then, the first cycle of the concurrent-chains schedule began in which a single VI 30-s schedule arranged access to the terminal links (the outcome phase). If a rat did not respond to either the right or left lever for 1 min during the choice phase, then both levers were retracted, the center lever was inserted, and the concurrent-chains schedule (i.e., the VI timer) stopped operating until after a response to the center lever

occurred (the rest phase). Each interval of the VI tape was derived from the distribution described by Fleshler and Hoffman (1962). A single VI schedule was used to equate reinforcement rate for the two alternatives. In this procedure, the available terminal link was assigned equally to the right or to the left lever in a quasirandom sequence. This procedure assured an equal number of presentations of each terminal link (e.g., Stubbs & Pliskoff, 1969).

When the terminal link became available on either lever, the VI timer stopped operating until after the reinforcer was delivered. Entry into a terminal link occasioned two events: (a) The lever retracted on the side not pressed, and (b) the lamp for the retracted lever was turned off. Further responding on the remaining lever produced food or no food according to a fixed-interval (FI) schedule in that terminal link. During the reinforcement period, the remaining lever was retracted and its lamp was turned off, and the food cup lamp was turned on for a prescribed period (9 s), irrespective of the number of food pellets delivered. For the constant alternative, a fixed number of pellets (i.e., three pellets) was delivered, and for the variable alternative a variable number of pellets was delivered, ranging from zero to ten, but with a mean of three pellets. Pellets were delivered into the food cup at a rate of one per 100 ms. Following the reinforcement period, both levers were inserted and another cycle of the concurrent-chains schedule began. The VI timer restarted at this time.

The VI schedule in the initial links was 2 s initially and was then increased to 30 s over several sessions. During this phase, the terminal links were FI 5-s schedules, and the reinforcement period was 3 s. In the first condition, rats chose between equal reinforcer amounts (one food pellet) under equal terminal-link schedules (FI 5 s). Each session lasted for 3 hr, and this condition continued for 15 sessions. Choice proportions with equal reinforcer amounts did not deviate from .5 by more than .05 for any rat; choice proportions for the right lever were .53, .54, and .48 for R22, R27, and R28, respectively.

Energy budgets. Energy budget was defined as positive when subjects' body weights were over 90% of their free-feeding weights and as negative when their body weights were under

80% of their free-feeding weights. Rats' body weights were increased to 90% of their free-feeding weights during the preliminary phase of training. In the condition of positive energy budget, the rats' body weights were increased to over 90% of their free-feeding weights by using the shorter terminal-link schedule (i.e., FI 20 s). In contrast, in the condition of negative energy budget, body weights were decreased to 80% of their free-feeding weights by using the longer terminal-link schedule (i.e., FI 70 s). Each value of the FI terminal links was determined based on a preliminary experiment. Two of the rats (R22 and R28) were initially exposed to the condition of negative energy budget and then to that of positive energy budget. For the remaining rat (R27), the order was reversed.

Variable reinforcer amount. The variability in number of food pellets delivered was based on a negative binomial distribution with parameters $k = 1$ and $p = .25$. This distribution has a larger variance than a Poisson (i.e., random) distribution with the same mean (Feller, 1968). The mean of three food pellets was used in Experiment 1 for the variable alternative. Actual distributions of food pellets for the variable alternative are shown in Figure 2. For the mean of three food pellets, the number of food pellets ranged from zero to ten pellets ($\sigma = 3.11$), and the coefficient of variation (i.e., standard deviation divided by the mean) was 1.04.

The rats chose between a constant and a variable three food pellets under positive and negative energy budgets. Each energy budget condition was replicated in two successive phases in which the side to which the variable alternative was assigned was reversed to control for position bias. Each phase of each energy budget condition lasted for 15 sessions; therefore, each energy budget condition consisted of a total of 30 sessions. These numbers of sessions were used because a preliminary experiment revealed that choice was stable after 10 sessions. When energy budgets were changed from positive to negative (or from negative to positive), a period of 1 week was inserted between two phases to adjust the level of body weight. Sessions were conducted 6 days per week, and on the remaining day enough food was provided freely (if necessary) to adjust the level of body weight.
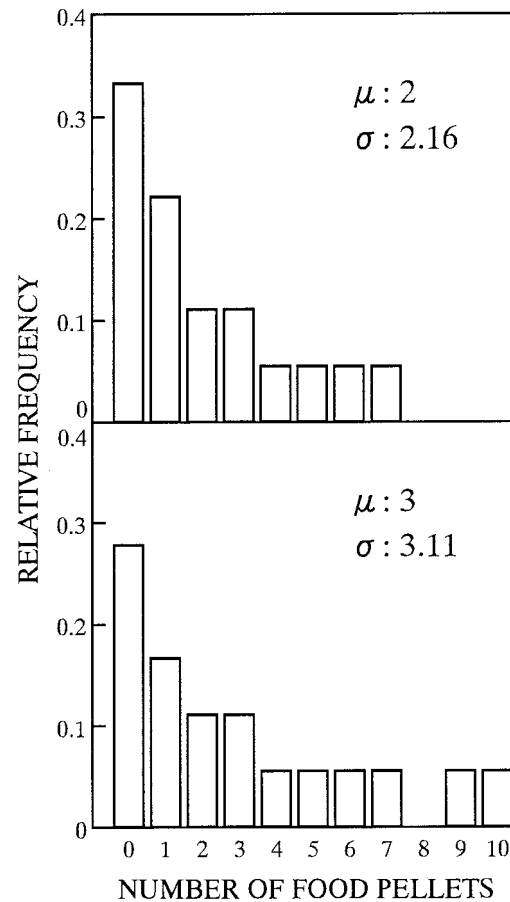

Fig. 2. Distributions of food pellets based on the negative binomial distribution. The upper panel shows the mean of two pellets, and the lower panel shows the mean of three pellets. Standard deviations are also presented.

RESULTS

Table 1 shows mean number of responses for both initial and terminal links, mean choice proportions and standard deviations, mean number of food pellets, working time in which the concurrent-chains schedule was in effect (i.e., time not counting the rest period), body weights ±90% of free-feeding weights and standard deviations, and percentages of free-feeding body weights. Data were calculated over four sessions based on the last two sessions of each phase of positive and negative energy budgets for each rat. Mean choice proportions were obtained by dividing the initial-link responses for the variable alternative by the total number of initial-link responses. The sequence of condi-

Table 1

Sequence of conditions, number of initial- and terminal-link responses, mean choice proportion for the variable reinforcer and standard deviation (in parentheses), mean number of food pellets, working time, and body weights for each rat in Experiment 1.

				Responses			
				Initial link		Terminal link	
	Reinforcer						
Subject	Variable	Constant	Energy budget	Variable	Constant	Variable	Constant
R22	3	3	Negative	903	1,124	2,307	2,300
			Positive	694	1,203	300	292
R27	3	3	Positive	552	1,443	425	473
			Negative	610	581	5,068	4,408
R28	3	3	Negative	695	620	2,588	2,682
			Positive	1,198	1,715	766	686

tions represents the order in which subjects were exposed to the two different energy budget conditions. Obtained choice proportions are derived from counterbalancing position bias, because the side to which the variable alternative was assigned was reversed in two successive phases of each energy budget condition.

Positive and negative energy budgets were well maintained by varying the equal terminal-link schedules. Body weights were gradually increased or decreased during the first phase of each energy budget and were maintained at asymptotic levels required by each energy budget condition. The number of food pellets obtained ranged from 386 (17.4 g) to 460 (20.7 g) for the positive energy budget, whereas it ranged from 204 (9.2 g) to 249 (11.2 g) for the negative energy budget. As for working time, there was a difference between positive and negative energy budgets; working time was relatively shorter under the positive energy budget than under the negative energy budget. The proportions of working time in the positive energy budget ranged from .73 to .89 of the session time (i.e., 3 hr), whereas they ranged from .96 to .98 in the negative energy budget; mean proportions of working time across all 3 rats were .83 for the positive energy budget and .97 for the negative energy budget.

Figure 3 shows the choice proportions for the variable alternative and body weights under positive and negative energy budgets. For all 3 rats, choice proportions for the variable three pellets differed between positive and negative energy budget conditions. Choice proportions were less than .5 when the en-

ergy budget was positive, and they were around .5 when it was negative. Mean choice proportions across the 3 rats were .357 under the positive energy budget and .524 under the negative energy budget. Thus, the rats preferred the constant three pellets in the positive energy budget, whereas they were indifferent between the constant and variable three pellets in the negative energy budget.

As shown in the right panel of Figure 3, changes in body weights satisfied the definition of energy budget; body weights increased or decreased from the 90% level of free-feeding weights to the level required by the two energy budget conditions. Body weights were over 92% of free-feeding weights under the positive energy budget and below 80% under the negative energy budget (see Table 1).

DISCUSSION

The results of Experiment 1 demonstrated that the rats' behavior was sensitive to changes in energy budget defined by the level of body weight and also was sensitive to the variability in amount of food. The rats preferred the constant three pellets when energy budget was positive, and they were indifferent when energy budget was negative. This finding is in part consistent with the results of the Caraco et al. (1980) study; that is, the present finding is consistent with the results Caraco et al. obtained in the positive energy budget, whereas it is inconsistent with those obtained in the negative energy budget.

Caraco and Lima (1985), using 4 dark-eyed juncos as subjects, studied the interaction of mean and variability with various combinations of mean and variance of seeds under a

Table 1

(*Extended*)

Choice proportion	Number of food pellets	Working time (s)		Body weights	
		Off	On	g ± 90% level	% of ad lib weights
.471 (.10)	204	443	10,357	−46.5 (13)	78.2
.353 (.22)	386	2,886	7,914	+25.3 (12.3)	95
.294 (.08)	442	1,155	9,645	+8.5 (6.7)	92.1
.556 (.11)	249	414	10,386	−47 (4.1)	79.2
.545 (.10)	230	259	10,541	−42.5 (7.1)	79.7
.423 (.10)	460	1,289	9,511	+39.5 (10.8)	100

positive energy budget. In a series with choice between constant and variable three seeds ($\mu = 3$ and $\sigma = 3$), mean choice proportion for variable reinforcers was .250, showing that the juncos were risk averse in the positive energy budget. In a similar experiment, Caraco (1981) studied choice between constant and variable reinforcers of the same mean under positive and negative energy budgets. The mean choice proportion for the variable three seeds across 3 dark-eyed juncos was .133 when the energy budget was positive, whereas it was .864 when the energy budget was negative. Also, Caraco (1983), using 3 white-crowned sparrows, arranged three different variabilities of the same mean and found that

mean choice proportion for the variable three seeds, averaged across three variability conditions ($\sigma = 1$, $\sigma = 2$, and $\sigma = 3$), was .252 when the energy budget was positive, whereas it was .637 when the energy budget was negative. The standard deviations of choice proportions were relatively large for both energy budgets, .20 and .27 for positive and negative energy budgets, respectively. These results showed that the granivorous birds, juncos and sparrows, were risk averse or risk prone, depending on energy budget.

Taken together, degree of preference was larger in the Caraco studies than in the present experiment. However, a comparison in which similar conditions of mean and vari-
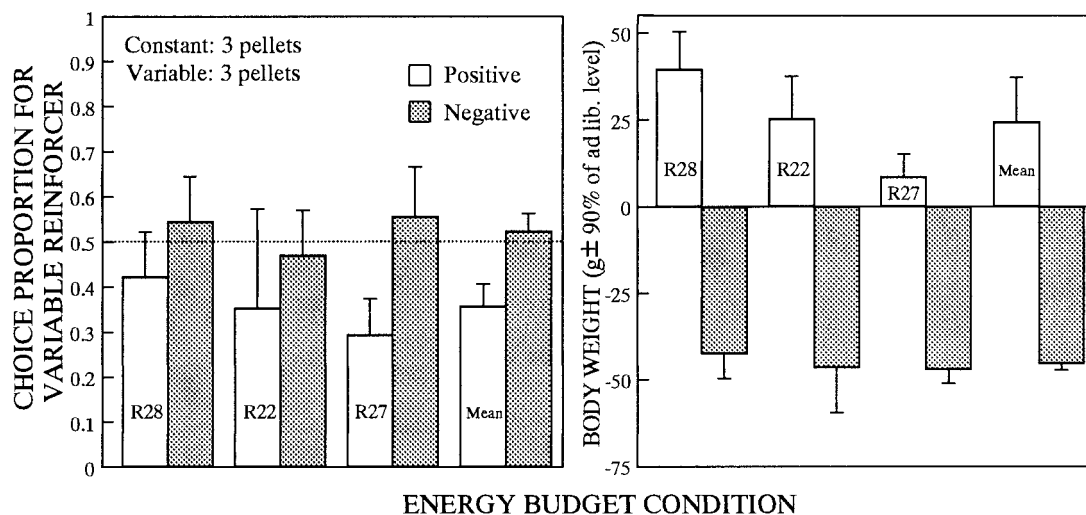

Fig. 3. Mean choice proportions for the variable three pellets (left panel) and body weights (in grams deviation from the 90% level of free-feeding body weights; right panel) under positive and negative energy budgets for each rat in Experiment 1. Filled bars show the negative energy budget condition, and open bars show the positive energy budget condition. Error bars represent one standard deviation.

ance ($\mu = 3$ and $\sigma = 3$) were studied in the Caraco (1983) study and the present one revealed that mean choice proportions for the variable three seeds were .287 for the positive energy budget and .533 for the negative energy budget. These values are close to those obtained in the corresponding condition of the present experiment; that is, mean choice proportions were .357 and .524 for the positive and negative energy budgets, respectively. Therefore, the present results are consistent with those obtained with sparrows (Caraco, 1983), although there are several procedural differences between the present study and the Caraco study. This pattern of results suggests that small granivorous birds such as sparrows as well as small mammals such as rats are primarily risk averse when the energy budget is positive.

The present findings and the results obtained with various combinations of mean and variance (Caraco & Lima, 1985) lead to the questions of whether the choices made by small mammals such as rats are sensitive to the differences in the number of food pellets and whether these sensitivities are affected by energy budgets (defined by level of body weight) in a manner similar to that found with small granivorous birds such as juncos and sparrows (Caraco, 1981, 1983; Caraco & Lima, 1985). Experiment 2 addressed these questions.

EXPERIMENT 2

METHOD

Subjects and Apparatus

Four male albino rats of the Wistar strain, approximately 3 months old at the beginning of the experiment, were housed individually in the chamber under a 12:12 hr light/dark cycle. As in Experiment 1, the rats were weighed before each session and were maintained at under 80% or over 90% of their free-feeding body weights, depending on energy budget conditions. They had no experimental histories. Water was continuously available in the chamber. The apparatus was the same as that used in Experiment 1 except for the use of four identical chambers.

Procedure

The basic procedure was the same as that used in Experiment 1 except for the reinforcer amounts and FI terminal-link schedules. Reinforcer amounts were varied in two conditions. In one condition, rats chose between a constant three pellets and a variable two pellets under positive and negative energy budgets, whereas in the other condition, rats chose between a constant two pellets and a variable three pellets under both energy budgets. As in Experiment 1, the number of food pellets per reinforcement was based on the negative binomial distributions with $k = 1$ and $p = .333$ for the mean of two pellets and $k = 1$ and $p = .25$ for the mean of three pellets. For the mean of three pellets, the number of pellets delivered ranged from zero to ten, whereas it ranged from zero to seven for the mean of two pellets (see Figure 2). Degree of variance was approximately equalized between the two conditions of variable reinforcer amounts (i.e., means of two and three pellets); that is, coefficients of variation were 1.04 for the mean of three pellets and 1.08 for the mean of two pellets.

All rats were initially given a choice between the constant three pellets and the variable two pellets, and then were given a choice between the constant two pellets and the variable three pellets under both energy budget conditions. Body weights were increased or decreased by varying the equal terminal-link lengths; for the positive energy budget, FI 5-s terminal-link schedules were used, whereas FI 40-s terminal-link schedules were used for the negative energy budget. As in Experiment 1, the values of the FI terminal links were determined based on a preliminary experiment. Each phase of each energy budget condition lasted for 15 sessions; therefore, each energy budget condition consisted of a total of 30 sessions. Each session lasted for 3 hr. Sessions were conducted 6 days per week, and on the the remaining day enough food was provided freely (if necessary) to adjust the level of body weight.

RESULTS

Table 2 shows the mean number of responses for both initial and terminal links, mean choice proportions and standard deviations, mean number of food pellets, working

time in which the concurrent-chains schedule was in effect (time excluding the rest period), body weights ±90% of free-feeding weights and standard deviations, and percentages of free-feeding body weights. As in Experiment 1, data were averaged across four sessions based on the last two sessions of each phase of the positive and negative energy budgets for each rat. Obtained choice proportions are the result of counterbalancing position bias because the side to which the variable alternative was assigned was reversed in the two phases of each energy budget condition.

As in Experiment 1, positive and negative energy budgets were well maintained by varying equal terminal-link lengths for both reinforcer amount conditions except in a few cases (the negative energy budget of R25 under the variable two pellets and constant three pellets condition, and the positive energy budget of R21 and the negative energy budget of R25, R26, and R30 under the variable three pellets and constant two pellets condition). Except for these cases, the number of pellets obtained ranged from 347 (15.6 g) to 469 (21.1 g) under the positive energy budget, whereas it ranged from 240 (10.8 g) to 288 (13 g) under the negative energy budget across both reinforcer amount conditions. The difference in working time between the two energy budget conditions was larger in Experiment 2 than in Experiment 1. The proportions of working time ranged from .51 to .80 of the 3-hr session for the positive energy budget, whereas they ranged from .80 to .99 for the negative energy budget. Mean proportions of working time across all 4 rats and reinforcer amount conditions were .67 of the session time for the positive energy budget and .94 for the negative energy budget.

Figure 4 shows the choice proportions for the variable two pellets and the changes in body weights under both energy budgets. For all 4 rats, there was no major difference in choice proportion for the variable two pellets between positive and negative energy budgets, and choice proportions were less than .5 under both energy budgets. All rats preferred the constant three pellets over the variable two pellets under both energy budgets. Mean choice proportions across all 4 rats were .334 under the positive energy budget and .304 under the negative energy budget.

As shown in the right panel of Figure 4, body weights increased or decreased from the 90% level of free-feeding weights depending on energy budget conditions.

Figure 5 shows the choice proportions for the variable three pellets and the changes in body weights under both energy budgets. For all 4 rats, choice proportions for the variable three pellets differed between positive and negative energy budgets. Although the standard deviations of choice proportions were fairly large and overlapping, it is notable that for 3 of the 4 rats, choice proportions were very close to .5 under the positive energy budget, whereas for 3 of the 4 rats they were over .5 under the negative energy budget. Mean choice proportions across all 4 rats were .529 for the positive energy budget and .634 for the negative energy budget. As shown in the right panel of Figure 5, body weights increased or decreased from the 90% level of free-feeding weights depending on energy budgets, except for R21 under the positive energy budget condition.

DISCUSSION

The results of Experiment 2 revealed that rats' choices were sensitive to changes in energy budgets and to the variability in amounts of food. The rats preferred the constant three pellets over the variable two pellets under both energy budgets, whereas they preferred the variable three pellets over the constant two pellets when the energy budget was negative but were indifferent when the energy budget was positive. More specifically, the present results demonstrated that the rats' choices were sensitive to the small difference in the number of pellets (i.e., when the difference was only one pellet).

The present results may be compared with those of Caraco and Lima (1985) for the conditions in which 4 dark-eyed juncos chose between a constant two seeds and a variable three seeds under a positive energy budget. They found that mean choice proportion for the variable three seeds changed from .931 to .510, to .812, and then to .352 as the variance for the variable three seeds increased (from $\sigma = 2$ through $\sigma = 2.4$, to $\sigma = 2.5$, and then to $\sigma = 3$).

Comparing the condition of similar mean and variance (i.e., $\mu = 3$ and $\sigma = 3$) with the present one (i.e., $\mu = 3$ and $\sigma = 3.11$), the

Table 2

Sequence of conditions, number of initial- and terminal-link responses, mean choice proportion for the variable reinforcer and standard deviation (in parentheses), mean number of food pellets, working time, and body weights for each rat in Experiment 2.

| | Reinforcer | | | Responses | | | |
| | | | | Initial link | | Terminal link | |
Subject	Variable	Constant	Energy budget	Variable	Constant	Variable	Constant
R21	2	3	Positive	1,283	2,086	139	131
			Negative	1,610	3,282	2,323	2,547
	3	2	Positive	1,901	2,534	418	430
			Negative	2,227	1,996	2,241	1,904
R25	2	3	Negative	713	1,222	1,437	1,669
			Positive	1,220	2,885	208	188
	3	2	Positive	2,752	1,594	740	627
			Negative	3,423	1,570	2,584	2,503
R26	2	3	Negative	612	1,945	2,518	3,449
			Positive	780	2,656	115	125
	3	2	Negative	3,424	1,359	3,275	2,745
			Positive	2,428	2,541	570	504
R30	2	3	Positive	1,382	2,057	441	434
			Negative	1,432	3,593	2,138	2,160
	3	2	Negative	2,935	1,670	2,702	2,581
			Positive	2,374	1,359	263	227

juncos preferred the constant two seeds over the variable three seeds in the positive energy budget. This result is inconsistent with the present results (i.e., all but 1 rat showed indifference). However, only 2 of the 4 juncos actually showed risk aversion; the remaining 2 juncos were indifferent or risk prone. Based on individual data, therefore, it seems questionable to draw any conclusions from the results obtained by Caraco and Lima (1985). Furthermore, the present experiment studied choice between a variable two pellets and a constant three pellets. If rats are risk averse, then they should prefer the constant three pellets. The present results confirmed this prediction: All 4 rats preferred the constant three pellets under both energy budgets.

GENERAL DISCUSSION

The present study, using a modified concurrent-chains schedule, investigated whether rats' preferences for variable amounts of food based on the negative binomial distribution depend on level of body weight in a closed economy. Experiment 1 studied choice between a constant and a variable alternative having the same mean under two different energy budgets and found that rats preferred the constant alternative under the positive energy budget and were indifferent under the negative energy budget. Experiment 2 studied choice between a constant and a variable alternative differing in the number of food pellets under two different energy budgets. The rats' choices were sensitive to the difference in the number of food pellets between constant and variable alternatives, and also were sensitive to the difference in the level of body weights (energy budgets). These results reveal that level of body weight as a measure of energy budget as well as number of food pellets influence choice for variability in amount of food.

With respect to the manipulation of energy budget, the present study demonstrated that rats' choices were sensitive to the difference in energy budgets defined by the level of their body weights. Mean choice proportions for the variable three pellets increased from .357 to .524 in Experiment 1 and from .529 to .634 in Experiment 2 with changes in energy budgets from positive to negative. These findings are consistent with those from small granivorous birds such as sparrows and juncos (Caraco, 1983; Caraco & Lima, 1985) and small mammals such as round-eared elephant shrews (Lawes & Perrin, 1995). Thus, these results support the present manipulation of

Table 2

(*Extended*)

Choice proportion	Number of food pellets	Working time(s)		Body weights	
		Off	On	g ± 90% level	% of ad lib weights
.383 (.28)	367	3,681	7,119	+19 (8.7)	94.3
.346 (.09)	288	893	9,907	−57.5 (5.2)	79.8
.524 (.33)	276	5,275	5,525	−6.8 (5.4)	88.5
.550 (.19)	240	2,169	8,631	−46.8 (2.2)	79.8
.340 (.20)	295	63	10,737	−37 (5)	80.3
.328 (.17)	469	2,407	8,393	+29.3 (6.6)	97.5
.506 (.25)	390	3,322	7,478	+31 (4.7)	97.9
.648 (.24)	295	186	10,614	−12 (3.5)	86.8
.236 (.02)	278	18	10,782	−40.3 (3.7)	79.7
.235 (.12)	366	3,757	7,043	+4 (2.1)	90.8
.708 (.06)	323	147	10,653	−26 (5)	83.3
.479 (.02)	347	4,162	6,638	+14 (12.7)	93.6
.390 (.05)	437	2,190	8,610	+36.8 (8.8)	97.7
.313 (.15)	281	932	9,868	−57 (16.4)	78.1
.628 (.04)	305	297	10,503	−47.3 (8.2)	80.2
.607 (.06)	369	4,031	6,769	+4 (5)	90.8

level of body weight as a valid measure of animals' energy budgets.

The present study varied the length of equal terminal links, whereas previous studies have used other procedures to manipulate energy budgets, such as deprivation period, length of intertrial intervals, number of trials during a session, rate of reinforcement, and

so on. Although these procedures necessarily produce different levels of body weight, only a few studies have referred directly to the level of body weight resulting from these procedures (Battalio et al., 1985; Hastjarjo et al., 1990; Kagel et al., 1986). For example, Hastjarjo et al. manipulated energy budgets by varying the number of free-choice trials in a
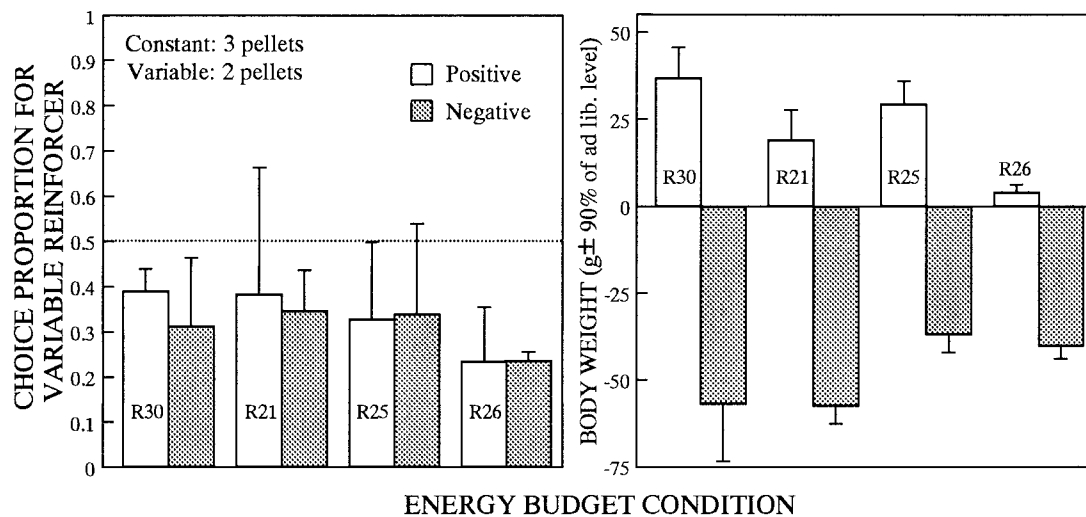

Fig. 4. Mean choice proportions for the variable two pellets (left panel) and body weights (in grams deviation from the 90% level of free-feeding body weights; right panel) under positive and negative energy budgets for each rat in Experiment 2. Filled bars show the negative energy budget condition, and open bars show the positive energy budget condition. Error bars represent one standard deviation.
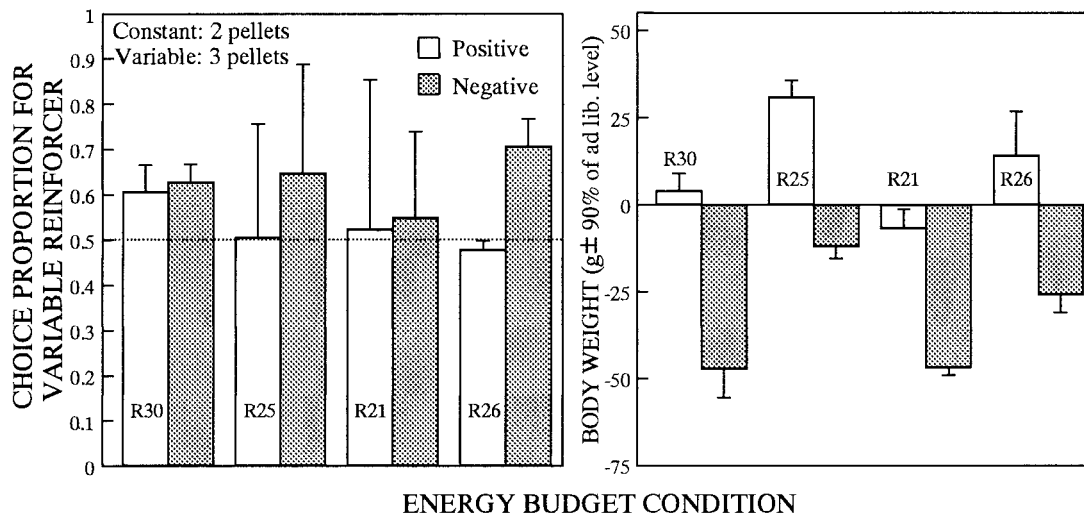
Fig. 5. Mean choice proportions for the variable three pellets (left panel) and body weights (in grams deviation from the 90% level of free-feeding body weights; right panel) under positive and negative energy budgets for each rat in Experiment 2. The labels are the same as in Figure 4. Error bars represent one standard deviation.

closed economy and found that although rats' body weights decreased as the number of free-choice trials decreased from 138 to 41 trials, rats' preferences for variable food pellets were the opposite of the predictions based on the energy budget rule (e.g., Caraco et al., 1980). That is, as body weight decreased, preference for the variable food decreased. Although Hastjarjo et al.'s findings do not support the predictions of the energy budget rule, the results might have been affected by some procedural problems inherent in their study. As shown in their Figure 3, rats' body weights were actually greater than their free-feeding weights in all conditions. Therefore, the failure to show changes in preferences as predicted from the energy budget rule may be explained in terms of the level of body weight obtained. In any case, as demonstrated in the present study, it seems necessary to show a correlation between decreases in level of body weight and increases in risk proneness (or decreasing risk aversion) if the energy budget defined by level of body weight is to be considered a factor in larger birds and mammals such as pigeons and rats.

The present experiments modified the standard concurrent-chains procedure to simulate foraging in the wild. The results revealed that the proportion of working time rats engaged in foraging was smaller under the positive energy budget than under the negative energy budget, although the experiments did not identify any of the other activities engaged in during the rest phase. It seems reasonable to assume that animals in the wild would allocate more of their behavior across different options such as mating, breeding, and defending territories in addition to foraging when their energy budget is positive. These findings have implications for experimental analyses of foraging. First, the present procedure provides one way of studying foraging relative to other activities. In a sense the present procedure may permit the study of foraging behavior uncontaminated by other activities, although the ocurrence of other activities was limited in the laboratory setting. Second, recent risk-sensitive foraging theories have been extended to apply to various foraging situations (see McNamara & Houston, 1992, for a review). Some models (e.g., Barnard, Brown, Houston, & McNamara, 1985; Houston & McNamara, 1985) deal with interrupted and uninterrupted foraging; environmental and behavioral events such as the presence of a predator or mating may make animals unable to forage for some period of time. In this respect, the present procedure, which included a rest phase, may provide a basis for testing predictions of the interruption models.

Recent theoretical discussion of sensitivity

to variability in amount of food has argued that risk-prone behavior is not necessarily optimal for minimizing the probability of starvation, even under a negative energy budget (McNamara, 1996; see McNamara & Houston, 1992, for a review). For example, McNamara (1996) proposed a model dealing with variability in amount of food in which it is assumed that an animal chooses between two alternatives having the same mean but differing in variability based on the distribution of a two-valued outcome (e.g., six seeds with probability .5 or no seeds with probability .5 for a variable outcome; Caraco et al., 1980). This model evaluates survival probabilities under the following three choice strategies in an experimental setting: (a) choosing only a certain alternative; (b) choosing only an uncertain alternative; and (c) choosing both certain and uncertain alternatives. According to the model, the first strategy is very important because the survival probability under the third strategy does not exceed that under the first strategy by more than 15%, whereas the survival probability under the second strategy is only comparable to that under the third strategy even in a negative energy budget. Therefore, an animal in a positive energy budget would show a preference for the certain alternative, whereas the animal in a negative energy budget would show indifference. Although the distribution function of food used in the present study (i.e., a negative binomial distribution) differed from that assumed in the model (i.e., the distribution of a two-valued outcome), the model's predictions are consistent with the present results with rats and with results obtained from different species in a laboratory setting (Caraco, 1983, white-crowned sparrows; Caraco & Lima, 1985, dark-eyed juncos; Lawes & Perrin, 1995, round-eared elephant shrews) and in a field experiment (Barkan, 1990, black-capped chickadees).

The present study employed the negative binomial distribution of food pellets (skewed distribution) because this distribution is thought to represent that experienced by many species in the wild (Iwasa et al., 1981; Pielou, 1969). In contrast, previous studies have used a simpler distribution of food represented by a two-valued outcome (e.g., Caraco et al., 1980). It is, however, unclear at present how differences in distributions of food

affect animals' choice for variability in amount of food. In this regard, Caraco and Chasin (1984) demonstrated that white-crowned sparrows were sensitive to the difference in skew of the distribution of food based on the normal distribution, although their response to skew was not as strong as was their response to variance in the distribution of food. Additional studies should examine the effect of different distributions of food, such as the Poisson (random distribution), binomial (regular distribution), negative binomial (skewed distribution), and a simple distribution represented by a two-valued outcome, in order to understand further the details of foraging behavior in the wild (Barnard et al., 1985; Caraco & Chasin, 1984; Iwasa et al., 1981).

The present experiments varied the lengths of the terminal links of a concurrent-chains procedure so as to produce different levels of body weight. Several studies have demonstrated a terminal-link effect, namely that the longer the length of equal terminal links, the greater the choice proportion for a preferred outcome (Duncan & Fantino, 1970; Ito, 1985; Ito & Asaki, 1982; Williams & Fantino, 1978). Could the terminal-link effect explain the results of Experiment 1? The terminal-link effect predicts that the degree of preference for the constant alternative (if the constant alternative is preferred) should be greater in the negative energy budget (FI 70 s) than in the positive energy budget (FI 20 s) condition. However, the present results were the opposite of the terminal-link effect and instead reveal that energy budget defined by the level of body weight influences rats' choices for variability in amount of food pellets.

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